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Foslie, M., 1884. Ueber die Laminarien Norwegens. (Christiania Vidensk. Selsk. Forhandl., 1884, No. 14.)

Guignard, Léon, 1892. Observations sur l'appareil mucifère des Laminariacées. (Ann. sci. nat. ser. 7, tome 15.)

Harvey, W. H., 1852. Nereis Boreali-Americana, Part I, Melanospermeæ.

Kjellman, F. R., 1877. Bidrag till kännedomen af Kariska hafvets Algvegetation. (Öfvers. af Vetenskaps-Akademiens Förhandlingar, 1877, No. 2.)

 Kjellman, F. R., 1883. The Algæ of the Arctic Sea. (Kongl. Svenska Vetenskaps-Akademiens Handlingar, Bandet 20, No. 5.)
Rosenvinge, L. Kolderup, 1893. Grønlands Havalger. (Meddelelser om Grønland, III.)

 Rosenvinge, L. Kolderup, 1894. Les Algues marines du Groenland. (Ann. sci. nat., ser. 7, tome 19.)
Rosenvinge, L. Kolderup, 1898. Deuxième Mémoire sur les Algues marines du Groenland. (Meddelelser om Grønland, XX.).

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REVERSIONS IN BERBERIS AND SAGITTARIA.

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(Plate 19.)

THAT single individuals should recover characters lost, or at any rate intermitted for generations, is certainly a highly remarkable fact, for which we cannot as yet very clearly account. Thus in cattle spots of peculiarly colored hair sometimes appear that can be definitely traced to ancestors several generations removed. In horses, faint zebrine stripes — characters evidently of considerable antiquity — sometimes come on the shoulders, flanks, and legs, especially in colthood. These and a large body of similar cases of reversion are of course familiar to everyone through the writings of Darwin.

Darwin noted a peculiar instance of reversion in a species of Melilotus. In this genus the leaflets, in assuming the sleeping position, twist on their stalks, and during the night stand with surfaces vertical, one edge presented to the sky, the other to the earth. This is the case with fifteen species observed by Darwin. In one instance, however, a deviation was noted : new shoots from some cut-down plants at first acted, not like Melilotus, but like Trifolium, in which genus the customary sleep-movements are executed by the sharp upward bending of

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the petiolules, so that the leaflets remain during sleep with their apices pointing toward the zenith. Darwin regarded this as probably due to the resumption of a primordial habit inherited from a remote ancestor allied to and sleeping like a Trifolium.¹

The word "reversion" commonly means to us the reappearance of a long-lost character, or at least of some peculiarity which has jumped one or two, or a few generations. But there is no essential difference between reversions in this restricted sense, and the ordinary reproduction, without intermission, of the racial likeness from generation to generation. All the features of the adult, as regards form, color, etc., are at each generation absolutely obliterated in the first, or unicellular, stage of the offspring. No length of years or passing of generations could make the obliteration more complete. The gap between the perfected parent form and the unicellular offspring is one compared with which the transition from the zebra-horse to the modern species is trifling. When the multitudinous peculiarities of form, color, temperament, action, of structure external and internal, survive the plunge and come safely through one such down-sinking of the organization, there is little increase of wonder — as there is no difference in the essential process — when one or another of these peculiarities delays a little in

coming to light again, under the form of what we call a reversion.

Again, we think of reversions as characters that become fixed in the individual, when they appear. The reverting pigeon permanently retains its slate-colored plumage, the reverting sheep its dun-colored or black fleece. In plants a reversionary leaf is a matured-leaf — it may be on an immature plant — differing from the "full character" leaf, and owing its form to the revival — as we say — of an ancestral impulse. But it is a familiar story that in the history of any living thing an orderly series of figures from the past appears, transient revivings of old groups, — systematized reversions. The phenomena of inheritance are all of one sort, whether the reappearing traits are permanent or not, and whether they occur regularly or only occasionally.

In the development of any individual we have thrown before us dissolving views of extinct, precedent races; views for the most part indifferently focused, but clear enough to give us most important information of the natural affinities, along old lines, of the developing form. In both branches of biological science this has, of course, long been recognized, and studies of development have been most fruitful. Both ¹ The Power of Movement in Plants, p. 347.

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embryonic and post-embryonic stages have been attended to, but the former by far the most thoroughly in both Zoölogy and Botany.

In Botany investigations of the young stages subsequent to the formation of the embryo, in order to discover hints of relationship that must disappear at a little later date in the life history, have been relatively few. But several workers are now paying attention to the matter, with good results. Some of the most interesting discoveries are coming from investigations of the minute anatomy of seedlings.

It scarcely need be said that the subject of reversions is of great importance in the study of the processes of heredity; and that in some respects plants make better subjects than animals in inquiries concerning the laws of reversion. Leaf-forms, in general simple, but in enough cases not simple to excess, are fit subjects for such inquiries.

BERBERIS. In Figure 1 of the accompanying plate I have represented a two-months' seedling of Berberis vulgaris. Were the young plant found growing wild, and at a distance from mature plants of the species, its parentage might not be suspected, the leaves are so unlike those of the adult condition in respect to the length of the petiole and the shape of the blade. The blade of the latter, or full leaf, is broader toward the apex and tapers very gradually to its junction with the extremely shortened petiole. The youthful lamina reverses this, being narrower above and more or less cordate at the base. It is distinctly jointed to the well-developed petiole, the earlier and later leaves thus agreeing in being unifoliolate. Bushes of this species, four years old, from which I collected leaves last fall, still showed the leaf-character of the seedling in preponderance over shorter-petioled forms approaching the adult type. And, on isolated branches of old bushes, I have this spring found persistent petioles much longer than the normal, the stalks, without much doubt, of similar reversionary leaves. For I look upon the "abnormal" forms as good examples of reversion.

We might guess that we have here the reappearance of an ancient type from its constant occurrence at the period of life when both plants and animals manifest ancestral traits. A like trait in the seedling of an allied species, *Berberis Thunbergii* (Fig. 3), makes the inference of a reversion still more plausible.

Of course the final and irrefutable evidence of reversion is the direct comparison of the form in question with an ancestral type preserved in the rocks. But ancestral types are preserved also in living

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Indeed all organic forms are either directly or remotely ancesforms. tral, the parents being ancestors one generation removed. Of several species having a common origin some are likely to keep original traits longer than others, and do, as is well known in some cases, maintain the aboriginal organization almost entire and unchanged for immense periods of time. The required ancestral type may therefore often be found in existent species; what is occasional - youthful, senile, or of sporadic occurrence — in one form, being the habitual and characteristic condition in some relative. This test of the reversionary nature of a particular youthful character, like the odd-shaped leaf of the Barberry seedling, must, as will be seen in the case of Sagittaria, be used with caution. In this case, however, the resemblance between the youthful leaf of B. vulgaris and the mature leaf of B. repens (Fig. 4) as regards both the length of the petiole and the shape of the terminal leaflet, seems to be well explained by supposing that the leaf of B. repens is very nearly like that of the progenitor of both B. repens and B. vulgaris; and that in youth our common species takes back to that progenitor, restoring the old form to the terminal leaflet, and the original rachis, but not the lateral leaflets.

Berberis vulgaris is a European and Asian form. B. repens is a western plant. B. Thunbergii is Japanese. Going to South America we find an interesting species for our present purpose in B. Agapatensis. The specimens examined were from Bolivia. Fig. 8 reproduces the outline of some of the mature leaves. In all but the somewhat lessened length of the petiole they agree with the seedling leaf of B. vulgaris. Most of the leaves of this species, however, show a little

tendency to acuteness at the base.

Berberis Thunbergii is particularly curious as to the marginal teeth. The first set of leaves after the cotyledons, about four or five, are entire, and devoid of spinous processes. Following these are an equal number rather coarsely toothed, the teeth bristly-pointed. The remaining leaves of the first year become more and more like the characteristic leaf, which again is smooth-margined, being without teeth and bristles. The smooth leaf, next to the cotyledons, does not seem to be an adaptation to any circumstance of the seedling period, but rather a reversion to a type possibly older than that represented in the infancy of *B. vulgaris*. The succeeding rough leaves, again, have no apparent adaptive relation to the seedling period, and probably revive 1900] Leavitt, — Reversions in Berberis and Sagittaria 153

a type now lost by B. Thunbergii, but retained in many species, — the bristly-margined type.

Berberis Thunbergii has by some authorities been treated as a variety of B. vulgaris. When we compare the seedlings we seem to find very positive evidence against any such assignment. If the two forms were so very closely related, their seedlings should be nearly or quite indistinguishable; we see on the contrary that they differ more markedly than the mature plants. A point to be noted in both forms is that the reverting leaves exhibit an added character, as compared with the leaves of the adult plant. It would be easy to dispose of many cases of suspected primordial structure simply as cases of arrested development, in the sense of aborted growth. But here the feeble, seedling plant produces organs in one respect more highly organized than like organs of the mature plant.

The trifoliolate leaves of B. repens, Figs. 4 and 5, are not the full character leaves of that species; though to judge from a good number of herbarium specimens examined they are of rather common occurrence. The prevailing leaves have five parts, or even seven. The contour of the end leaflet is then altered (Fig. 6).

If, as is likely, *B. vulgaris*, *B. Thunbergii*, and *B. Agapatensis* are really unifoliate, then the trifoliate leaf of *B. repens* is probably near the type from which they have all been derived by reduction. *B. Aquifolium*, a more complex form, reverts only occasionally from its more advanced position to the type characterized by the cordate terminal leaflet; at least in the adult plant.

SAGITTARIA. In estimating the value of youthful characters for the reading of family history, we must take into account the influence of the requirements of the seedling, as differing from those of the adult. The forms of cotyledons, for instance, are traceable to the form of the fruit, the need of storing nourishment, and the exigencies of confinement in small spaces. The contours rarely bear any relation to the contours of the ordinary foliage leaves, present or past. Similarly after germination the young plant may encounter problems that never recur subsequently, and meet these problems with specialized structures having no connection with ancestral mature types. In the Sagittaria, for example (Fig. 7), the interpretation of the linear first leaves (a, b, c) is complicated by the fact that the seedling is submerged, while the hastate or sagittate adult leaf is aërial. Was there ever a time when

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the Sagittarias possessed no more highly differentiated leaf than the present ribbon-form leaf of the seedling?

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It is easier to answer the question with reference to the spoonshaped intermediate leaf (d). In the old-age of the plant — that is, of any particular shoot of the branching rhizome in the species represented — the leaves retrace the course of development as the vegetative

vigor becomes exhausted and second childhood comes on. The series f, g, h Fig. 7, is a reversionary series, beginning with hastate forms more and more unlike the sagittate character leaf, and ending with very narrow-bladed lanceolate forms. These latter stand well out of water, so that the direct action of that medium is eliminated from the case, and even were there no other Sagittarias and the Alismas, we might be tolerably sure,—from the *double* appearance, in youth and in old age, — that the lanceolate form represents a return to what was once the farthest limit of differentiation.

The nature of the linear, grass-shaped early leaves of the seedlings and new shoots, which seem to be the same thing as the ultimate leaves of several species, is perhaps doubtful. They are spoken of by several writers as *phyllodia*. If the term has any distinctive meaning, it implies reduction from a bladed to a bladeless condition. The linear

leaves are looked upon as petioles, with the notion that a part normally produced in addition to and beyond these bodies is suppressed through the influence of the surroundings.

Seedling stages should throw light on the question. Sagittaria Montevidensis, of South America, passes through its seedling stages very slowly, and presents a very complete series of transitional forms. In these there is every indication that the lanceolate or elliptical blade (d) is derived from the linear forms not by addition at the tip, but by gradual differentiation of the terminal region of the linear leaf to form the ultimate blade, while the lower part of the original body (or blade) becomes gradually thickened and then rounded to make the ultimate petiole. If this is so, the grass-shaped early leaves are not reduced forms in the sense appertaining to the *phyllodia* of the Acacias. They are in fact probably not *phyllodia*; they seem to be early complete forms giving rise by progressive and structurally necessary steps to the adult differentiated leaf.

The linear leaves of the seedling, forming in this manner the basis of an evolution toward the full character leaf, seem little like cases of what the zoologists would call larval adaptation. It is probably not

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unreasonable to interpret them as reversions to a primitive type of Sagittaria. That prototype may have been a submerged plant. THE AMES LABORATORY, North Easton, Massachusetts.

EXPLANATION OF PLATE 19. Figure 1, a growing seedling of Berberis vulgaris. 2, characteristic leaf of the same species. 3, a pressed seedling of B. Thunbergii. 4, reversionary leaf common on B. repens. 5, one of six very large, 3-foliolate leaves on a sucker-like shoot of B. repens. 6, the character leaf of the same species. 7, stages in the development of Sagittaria Montevidensis: a, b, c, d, e progressive forms; the character leaf, sagittate, not represented; f, g, h regressive forms in exhausted shoots.

THE OCCURRENCE OF THAMNOLIA IN MAINE.—The rare alpine lichen Thamnolia has not before been reported from Maine, and the following note may be of interest. In August, 1896, the writer collected near the summit of Mt. Washington, New Hampshire, the typical form of Thamnolia vermicularis (Sw.) Schaer.; and in September, 1898, an interesting form of the same species was found near the summit of Mt. Katahdin in Maine. Specimens of the latter form were sent to Miss Cummings, who determined them as Thamnolia vermicularis, var. subuliformis Schaer., and stated that in the Tuckerman Herbarium there was but one representative of the type. In habit of growth the variety is strikingly different from the type, this feature being more marked than the shape of the thallus. The type as collected on Mt. Washington was growing in densely cespitose bunches, and the variety, as on Mt. Katahdin, was not at all cespitose, but was very scattered, often isolated and intermixed with other lichens and mosses, notably with Cetraria Islandica. It was found only sparingly, and no specimens of the typical form were observed. This species resembles at first sight a dead or bleached form of some of the alpine species of Cladonia, but its color is very distinctive. Owing to its silvery gray shade and its subulate thallus it is a very beautiful and striking species. - ELMER D. MERRILL, Washington, D. C.

ASPIDIUM SIMULATUM IN NEW HAMPSHIRE. — Aspidium simulatum was illustrated and described by Mr. George E. Davenport in the latter part of 1896. Since that time it has been reported from comparatively few stations over a wide range. The writer is not aware that this fern has been reported from but two localities in New Hampshire, namely, Seabrook and Kingston. These towns are in close proximity,